Evolution of plant water-use strategies from isohydry to anisohydry: an eco physiological and evolutionary perspective

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Abstract. Plant water-use strategies represent a central axis of adaptation to environmental stress, particularly under the increasing frequency and intensity of drought associated with global climate change. Traditionally framed as a dichotomy between isohydric and anisohydric behavior, plant responses to water limitation are now recognized as part of a continuous and dynamic spectrum shaped by the integration of hydraulic architecture, stomatal regulation, and carbon assimilation processes. This study provides an eco-physiological and evolutionary synthesis of plant water-use strategies, emphasizing the transition from discrete classifications toward a continuum-based framework. We highlight that variation along the iso–anisohydric spectrum is governed by coordinated trait syndromes, including stomatal sensitivity, xylem vulnerability to cavitation, osmotic adjustment, and tissue elasticity, all of which are modulated by phylogenetic constraints and environmental filtering, particularly aridity. Importantly, these strategies are not static but exhibit significant temporal plasticity, shifting across seasonal, ontogenetic, and short-term stress scales in response to environmental variability. Such flexibility enables plants to optimize trade-offs between hydraulic safety and carbon gain, which are further embedded within broader plant economic spectra ranging from resource-acquisitive to resource-conservative strategies. At larger spatial scales, aridity emerges as a key selective force driving convergence in hydraulic traits across biomes, while within-community hydraulic diversity enhances ecosystem resilience to drought by stabilizing carbon and water fluxes. Conversely, reduced plasticity or functional diversity may increase vulnerability to extreme climatic events. Overall, this work underscores the need for integrative frameworks that move beyond static trait-based classifications to incorporate continuum dynamics, eco-evolutionary trade-offs, and context-dependent physiological responses. Such approaches are essential for improving predictions of vegetation dynamics and biosphere–atmosphere feedbacks under future climate scenarios characterized by intensified drought regimes.

Keywords: isohydry, anisohydry, plant water-use strategies, hydraulic traits, stomatal regulation, drought stress, water-use efficiency, eco-physiology, evolutionary ecology, temporal plasticity, aridity gradients.

Introduction. Understanding how plants regulate water use under conditions of environmental stress has become a central question in contemporary plant ecophysiology, particularly in the context of accelerating climate change and increasing aridity across many regions of the globe (Farooq et al., 2015; Riaz et al., 2017; Papuc & Bora, 2023). Plant water-use strategies are not governed by a single trait, but instead emerge from the dynamic integration of hydraulic architecture, stomatal regulation, carbon assimilation, and environmental constraints operating across multiple spatial and temporal scales (Kannenberg et al., 2022; Liang et al., 2023).

Traditionally, plant responses to drought have been described using the conceptual dichotomy of isohydric versus anisohydric behavior (Zhao et al., 2023). Isohydric species are characterized by relatively tight regulation of leaf water potential, primarily through early stomatal closure, thereby minimizing the risk of hydraulic failure (Liu et al., 2026). In contrast, anisohydric species allow greater fluctuations in water potential, maintaining gas exchange and carbon assimilation under declining water availability, albeit at the cost of increased vulnerability to xylem cavitation. While this framework has provided a useful heuristic, growing empirical evidence suggests that plant water-use behavior is better represented as a continuum rather than a discrete classification.

This continuum reflects coordinated variation in multiple functional traits, including stomatal sensitivity, xylem vulnerability, osmotic adjustment, and tissue elasticity. Importantly, these traits do not operate in isolation but are shaped by both phylogenetic constraints and environmental filtering, particularly along gradients of water availability. As a result, plant strategies must be interpreted within a broader eco-evolutionary context, where trade-offs between hydraulic safety, carbon gain, and growth are mediated by natural selection (Petrescu-Mag 2026ab).

Moreover, plant water-use strategies are inherently dynamic. They can shift seasonally, ontogenetically, or in response to extreme climatic events, reflecting the plasticity of physiological processes and the complexity of plant–environment interactions. This dynamic perspective challenges static trait-based classifications and emphasizes the need for integrative approaches that link physiological mechanisms to ecosystem-level processes.

In this work, plant water-use strategies are examined through an eco-physiological and evolutionary lens, with particular emphasis on the continuum between isohydric and anisohydric behavior. By synthesizing insights from hydraulic theory, trait-based ecology, and recent empirical studies, this paper aims to provide a comprehensive understanding of how plants balance water conservation and carbon acquisition under drought stress, and how these strategies are shaped by environmental gradients and selective pressures.

Continuum vs. Discrete Strategies. Multiple lines of evidence support a continuum rather than discrete isohydric/anisohydric categories. A hydraulic-index approach in a biodiverse shrub community showed continuous variation in the margin between stomatal closure (Pg12) and xylem cavitation (P50), linearly related to xylem safety margin (Skelton et al., 2015). Hydroscape metrics similarly place species along a continuous iso–anisohydric axis, linked to osmotic and turgor traits (Meinzer et al., 2016). A conceptual and quantitative re-evaluation of iso/anisohydry demonstrates that tight water-potential regulation is not consistently associated with stronger stomatal control or reduced assimilation, undermining simple categorical assignments (Martínez-Vilalta & Garcia-Forner, 2017). A recent review emphasizes that water-use “strategies” are emergent, highly dynamic responses shaped jointly by traits and environment, again favoring a continuum view (Kannenberg et al., 2022). At ecosystem scale, global satellite-based isohydricity also varies continuously with radiation, height, and seasonality, with land-cover classes poor predictors of discrete behavior (Konings & Gentine, 2017) (Table 1, Figure 1).

Table 1

Common quantitative axes underlying the iso–anisohydric continuum

Scale / metric	*Key idea*	*References*
Pg12–P50 (individual species)	Continuous stomatal–xylem safety spectrum	Skelton et al., 2015
Hydroscape area, ψpd–ψmin slopes	Continuous landscape of ψ regulation	Meinzer et al., 2016
ψ regulation vs. stomatal control	Weak categorical separation across species	Martínez-Vilalta & Garcia-Forner, 2017; Leuschner et al., 2021
Satellite ecosystem isohydricity (r)	Global continuous gradient with climate	Konings & Gentine, 2017.

Temporal Plasticity and Context-Dependent Shifts in Plant Water-Use Strategies. While the iso–anisohydric framework is often used to position species along a functional continuum, increasing evidence indicates that plant water-use strategies are not fixed properties but context-dependent expressions that vary across temporal scales (Martínez-Vilalta & Garcia-Forner, 2017; Zhang et al., 2024; Guo et al., 2019; Feng et al., 2019). This temporal plasticity reflects the capacity of plants to modulate physiological responses in accordance with fluctuating environmental conditions, thereby optimizing performance under variable and often unpredictable drought regimes (Mrad et al., 2018; Zhang et al., 2024; Guo et al., 2019; Lu et al., 2019; Wankmüller & Carminati, 2021).

At seasonal scales, many species exhibit shifts in stomatal regulation and hydraulic functioning in response to changing soil moisture, atmospheric demand, and phenological stage (Jin et al., 2023; Martínez-Vilalta & Garcia-Forner, 2017; Zhang et al., 2024; Sperry et al., 2017; Wang et al., 2024; Wang et al., 2025; Hartmann et al., 2021; Lu et al., 2019; Wankmüller & Carminati, 2021). For example, plants may adopt relatively anisohydric behavior during periods of resource abundance to maximize carbon gain, while transitioning toward more isohydric regulation during prolonged drought to preserve hydraulic integrity (Jin et al., 2023; Mrad et al., 2018; Zhang et al., 2024; Guo et al., 2019; Wang et al., 2024; Wang et al., 2025; Hartmann et al., 2021; Nolan et al., 2017; Feng et al., 2019). Such within-species variability complicates attempts to assign fixed hydraulic strategies and highlights the importance of environmental context (Martínez-Vilalta & Garcia-Forner, 2017; Zhang et al., 2024; Guo et al., 2019; Wang et al., 2025; Lu et al., 2019; Kavanagh et al., 1999; Feng et al., 2019).

Short-term responses to drought events further illustrate the dynamic nature of water-use regulation (Jin et al., 2023; Mrad et al., 2018; Sperry et al., 2017; Wang et al., 2024; Lu et al., 2019; Wankmüller & Carminati, 2021). Rapid adjustments in stomatal conductance, osmotic potential, and leaf turgor allow plants to buffer transient stress, although these responses may incur physiological costs, including reduced photosynthetic capacity or increased metabolic demand for osmotic adjustment (Jin et al., 2023; Sperry et al., 2017; Cardoso et al., 2018; Hartmann et al., 2021; Franklin et al., 2023; Nolan et al., 2017; Wankmüller & Carminati, 2021). The balance between these costs and benefits is likely to differ among species and environments, contributing to the diversity of observed strategies (Jin et al., 2023; Mrad et al., 2018; Zhang et al., 2024; Sperry et al., 2017; Cardoso et al., 2018; Wang et al., 2024; Wang et al., 2025; Lu et al., 2019; Wankmüller & Carminati, 2021).

Ontogenetic changes also influence water-use behavior (Beikircher et al., 2024; Kannenberg et al., 2021; Venturas et al., 2017; Kavanagh et al., 1999). Seedlings, for instance, often display more conservative water-use strategies due to their limited hydraulic capacity and vulnerability to desiccation, whereas mature individuals may tolerate greater fluctuations in water potential (Beikircher et al., 2024; Kannenberg et al., 2021; Venturas et al., 2017; Kavanagh et al., 1999). Additionally, structural changes in xylem architecture over the lifespan of a plant can alter vulnerability to cavitation and, consequently, the positioning along the iso–anisohydric continuum (Jin et al., 2023; Beikircher et al., 2024; Kannenberg et al., 2021; Cardoso et al., 2018; Venturas et al., 2017; Franklin et al., 2023; Kavanagh et al., 1999).

Importantly, temporal plasticity in water-use strategies has significant implications at the ecosystem level. Variability in species responses can enhance functional diversity, thereby stabilizing ecosystem processes such as transpiration and carbon uptake under drought conditions. Conversely, reduced plasticity may increase ecosystem vulnerability to extreme climatic events.

Overall, recognizing the temporal and context-dependent nature of plant water-use strategies is essential for advancing predictive models of vegetation responses to climate change. It underscores the need to move beyond static trait classifications toward frameworks that explicitly incorporate physiological flexibility and environmental variability.

Water-Use Efficiency–Growth Trade-offs. At the physiological level, a unified drought framework links a continuum from fast, water-spending, growth-maintaining strategies to slow, water-saving, survival-oriented strategies, mapping onto the "fast–slow" plant economics spectrum (Volaire, 2018). Isohydric behavior (early stomatal closure, larger hydraulic safety margins) generally enhances hydraulic safety but constrains carbon gain during drought, while anisohydric behavior maintains gas exchange at the cost of greater cavitation risk (Jin et al., 2023; Skelton et al., 2015). Global tree-ring analyses show that wood density and more negative minimum leaf water potential (traits associated with safety and conservative water use) correlate with stronger growth sensitivity to drought but also with particular resistance–recovery combinations, illustrating complex growth–safety trade-offs across species (Serra-Maluquer et al., 2022).

Water-use efficiency (WUE) itself is strongly context-dependent. Under drought, leaf-level WUE typically increases as stomata close, but canopy-scale transpiration-based WUE can decline because carbon uptake falls faster than water loss, and stomatal regulation cannot fully offset hydraulic constraints (Peters et al., 2018; Li et al., 2025). Across Europe, increasing intrinsic WUE in grasslands is driven mainly by increased gross primary production with regulated transpiration, while in some Central European regions declining intrinsic WUE signals impaired ecosystem performance (Terán et al., 2023).

Natural selection can favor low WUE, acquisitive strategies in arid and semi-arid systems when rapid growth and reproduction before severe drought maximize fitness. In semiarid Mediterranean gypsum shrubs, selection via reproduction consistently favored early phenology, low WUE, high specific leaf area, low leaf dry matter content, and high leaf nitrogen—traits of a drought-escape, fast resource-use strategy rather than a conservative one (Blanco-Sánchez et al., 2022). Similarly, in desert sunflowers, higher fitness in natural populations was associated with lower WUE, higher leaf N, larger and more succulent leaves, patterns consistent with dehydration escape or water "wasting" to enhance nutrient delivery (Donovan et al., 2007). In an invasive annual radish across an aridity gradient, populations from drier sites combined early flowering (escape) with increased root allocation (tolerance) and high resource-acquisitive leaf traits, indicating that escape and resistance syndromes can co-evolve rather than being mutually exclusive (Welles & Funk, 2021).

At the ecosystem scale, droughts in the Northern Hemisphere have produced coherent increases in WUE but concurrent reductions in net carbon uptake, revealing a macro-scale expression of the safety–growth trade-off: plants close stomata to save water, improving WUE, yet sacrifice regional carbon sequestration (Peters et al., 2018). A global eco-evolutionary optimality model further shows how soil nutrient acquisition strategies and aridity jointly shape the relative carbon cost of nutrient vs. water acquisition, integrating below-ground economics into water-use trade-offs (Cheaib et al., 2025).

Biome-Level Variation and Aridification as a Selective Filter. Aridity operates as a major selective driver of hydraulic and water-use traits across biomes. A global synthesis of 202 woody species shows coordinated declines in seasonal minimum water potential, turgor loss point, stomatal closure threshold, and xylem vulnerability with increasing aridity, implying co-selection for tighter regulation and greater embolism resistance in xeric regions (Jin et al., 2023). In dry sites, seasonal minimum water potentials fall below turgor loss point, with stomatal closure and high embolism resistance preventing catastrophic hydraulic failure—an effectively more isohydric, conservative sequence. In mesic regions, minimum water potentials remain safer relative to embolism thresholds, and stomatal closure can lag, yielding a riskier, more anisohydric sequence that maximizes carbon uptake (Jin et al., 2023).

A continental-scale study of Australian forests found strong coordination between leaf turgor loss, xylem embolism resistance, stomatal traits, and wood carbon investment across an aridity gradient. Species from drier sites exhibited more negative turgor loss points and greater embolism resistance, operating with somewhat larger hydraulic safety margins than species from wetter sites, but overall margins remained constrained, meaning forests across biomes function close to hydraulic limits and are vulnerable to intensified drought (Peters et al., 2021).

Biome-scale analyses using ecosystem isohydricity metrics reveal additional structure. Evergreen tropical broadleaf forests tend to be very isohydric, while croplands are highly anisohydric; however, most land-cover classes span wide ranges of behavior, and canopy height and local radiation explain more variation than biome identity alone (Konings & Gentine, 2017). In seasonally dry regions, many ecosystems shift towards more isohydric behavior in the dry season, but some tropical forests become more anisohydric during dry-season leaf flush, apparently exploiting transient resource windows at higher hydraulic risk (Konings & Gentine, 2017).

Hydraulic trait diversity within forests modulates ecosystem response to drought. Across temperate and boreal sites, higher diversity in xylem and stomatal traits buffers drought-induced variation in carbon and water fluxes, enhancing ecosystem resilience; in contrast, standard leaf and wood traits (e.g., specific leaf area, wood density) have weaker predictive power at this scale (Anderegg et al., 2018). This finding suggests that assemblages spanning a range of iso–anisohydric behaviors and hydraulic safety–efficiency combinations may be favored under increasingly variable and extreme drought regimes.

Finally, local desert shrub communities exemplify how anatomy-based strategies map onto environmental stress regimes. In the eastern Qaidam Basin, combinations of leaf–stem hydraulic efficiency vs. safety define "exploitative," "stable," and "opportunistic" strategies along gradients of sandy vs. salty vs. cold deserts, with leaves and stems partitioning roles in water transport vs. conservation (Liu & Zheng, 2024). These anatomically grounded syndromes sit naturally within the broader continuum of isohydric–anisohydric regulation and the ecological fast–slow spectrum (Volaire, 2018; Liu & Zheng, 2024).

Concluding Remarks. The present synthesis highlights that plant water-use strategies cannot be adequately understood through rigid categorical frameworks, but instead emerge as dynamic, multi-dimensional responses shaped by the interplay between hydraulic architecture, stomatal regulation, and environmental constraints. The traditional dichotomy between isohydric and anisohydric behavior, while conceptually useful, is increasingly superseded by a continuum-based perspective that better captures the diversity and flexibility of plant responses to water limitation.

Across this continuum, coordinated trait syndromes reflect fundamental trade-offs between hydraulic safety and carbon gain, which are further embedded within broader plant economic strategies ranging from resource-acquisitive to resource-conservative modes. These trade-offs are not fixed but are modulated by environmental gradients, particularly aridity, which acts as a powerful selective filter driving convergence in hydraulic traits across biomes. As a result, species in dry environments tend to exhibit tighter regulation of water potential and greater resistance to hydraulic failure, whereas species in more mesic conditions often operate closer to hydraulic limits in order to maximize productivity.

Importantly, this work emphasizes that plant water-use strategies are inherently dynamic. Temporal plasticity allows plants to shift their physiological behavior across seasonal, ontogenetic, and short-term stress scales, challenging static classifications and underscoring the importance of context-dependent responses. Such flexibility plays a critical role in determining individual fitness as well as ecosystem-level resilience under increasingly variable climatic conditions.

At larger spatial scales, the integration of hydraulic diversity within plant communities emerges as a key determinant of ecosystem stability. Assemblages encompassing a wide range of water-use strategies can buffer fluctuations in carbon and water fluxes during drought, thereby enhancing resilience. Conversely, systems characterized by reduced functional diversity or constrained plasticity may be more vulnerable to extreme events and long-term aridification.

Taken together, these findings point toward the need for a conceptual shift in plant ecophysiology, from static trait-based classifications to integrative frameworks that explicitly incorporate continuum dynamics, eco-evolutionary trade-offs, and temporal variability. Such approaches are essential for improving predictions of vegetation responses to global change and for understanding the future functioning of terrestrial ecosystems under intensifying drought regimes.

Future research should prioritize the integration of physiological, anatomical, and ecosystem-scale data, as well as the development of models capable of capturing the dynamic and context-dependent nature of plant water-use strategies. In doing so, it will be possible to better resolve the mechanisms underlying plant resilience and vulnerability, and to refine projections of biosphere–atmosphere feedbacks in a rapidly changing world.

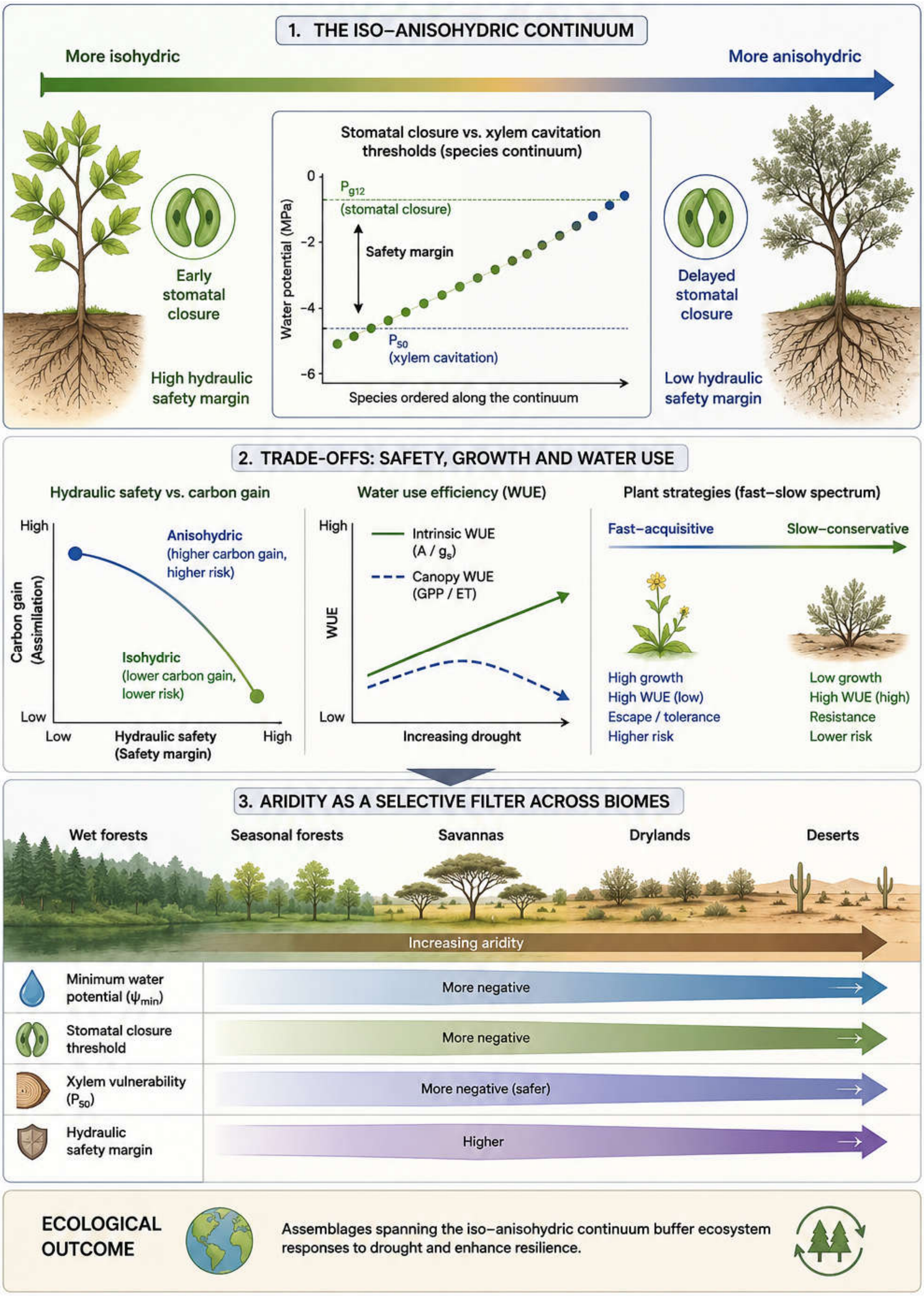

Figure 1. Evolution of plant water-use strategies from isohyry to anisohydry: a continuum shaped by trade-offs, selection and aridity.

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